The Development of Rice Grains under Controlled Environment I. The Effects of Temperature, its Daily Range and Photoperiod During Ripening on Grain Development

Tohoku Journal of Agricultural Research
Vol. 22, No. 2, August 1971
Printed in Japan

The Development of Rice Grains under Controlled Environment
I. The Effects of Temperature, its Daily Range and Photoperiod During Ripening on Grain Development

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(Received May 7, 1971)

Summary

Using outdoor phytotrons, a japonica rice Norin-17 and an indica type IR-8 were exposed after anthesis to maturity to day-temperatures of 35, 30, 25 and 20°C, and night-temperatures of 10 to 35°C at 5°C intervals, and to two photoperiods: 8-hr natural day light (SD) and 16-hr photoperiod (LD: SD plus 8-hr supplemental light)

Under higher temperatures except 35–35°C, the rate of ripening was higher but the inflow of assimilates into the grain ceased earlier, resulting in lower fruiting percentage, lower 1000-kernel-weight and thus in a smaller "ripening index". In contrast, under lower temperatures the rate was slower but ripening continued longer with the result of higher fruiting percentage and 1000-kernel-weight.

It may be concluded from the results that the optimum temperature conditions for ripening seemed to be 20°C or a little higher day temperature combined with a range of 5 to 10°C lower night temperature. Thus the optimum mean temperature may be 20°C or a little lower. The two varieties did not differ significantly in their response to these temperatures. The short day was inferior to the long-day for ripening.

Since the work of Sasaki (1918), there have been several reports published regarding the ripening of rice kernels under various temperature conditions. Matsushima et al (1–3) and Nagato et al (4–6) showed that under lower temperatures maturation proceeded smoothly and eventually formed well developed, good quality grains, although it took much time, while under increasingly higher temperatures maturation was progressively hastened with the consequence that the 1000-grain-weight and yield diminished with ill-ripened kernels. Matsushima and Wada (3) reported the optimum mean temperature for maturation to be 21 to 25°C.

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They (2–4) also showed that the lower night temperature would lead to an increased 1000-kernel weight.

The authors intended to ratify the above results by treating the whole plants under wider day-night temperature regimes than ever tried combined with 2 photoperiods from fertilization to maturity.

Materials and Methods

A japonica type Norin-17 and an indica type IR-8 were used. IR-8 was urged to flower by shortday treatment from the end of June to the middle of July under black vinyl cover. Seedlings of both varieties at the 6.5 leaf stage were transplanted to 20 cm pots on June 6, 1967, 2 hills per pot with 2 plants to each hill. The soil used was a river sand rich in clay. The nutrient solution containing $(NH_4)_2SO_4$, KCl and Na_2HPO_4 was renewed once a week after washing old solution off with tap water until the plant headed. Thereafter no fertilizer was applied.

Two pots totaling 4 hills were exposed to 2 daylengths and 4 day-temperatures with differential daily ranges. Two daylength treatments are shortday (SD):8-hr natural light from 9 am to 5 pm, and longday (LD): shortday plus 8-hr supplemental light with a 40-Watt incandescent lamp 1 m above plant tops.

Both short- and long-day phytotrons groups were covered with a half-cylinder roof at 5 pm and uncovered at 9 am, and long-day chambers were lighted when the roof covered the whole chambers. For temperature treatments 3 sets of 4 chambers, each chamber being maintained at 20, 25, 30 and 35°C day-temperatures, respectively, during 8-hr short-day periods, were used. One set was for short-day treatment and the other two for long-day treatment. Differential night temperature treatments from 10 to 35° at 5°C intervals were given by moving pots every day at 5 pm and 9 am from chamber to chamber controlled under long-day conditions. The relative air-humidity of each chamber was kept around 60 to 70 percent.

Before treatment, the flowers which opened at the same date were marked with ink and the plants were put outdoors one day to fertilize the flowers. Then the pots were moved to phytotrons and exposed to different conditions. The starting dates of treatment were August 7 (Norin-17), August 20 (IR-8, LD) and August 24 (IR-8, SD), respectively. After that, 3 to 4 culms each with about 30 inked flowers were sampled at weekly intervals to measure the trend of 1000-kernel-weight. On the other hand, each 5 to 7 culms per pot having uniform size, the most flowers of which completed fertilization and the rest flowers before flowering were dissected, were selected and exposed to the same conditions to compare the yield at maturity. The maturation date was determined by the fact that 90 percent in Norin-17 and 80 percent in IR-8, respectively, of pedicel numbers of each panicle turned yellow. The panicles and straws during ripening were analyzed for total nitrogen by a semi-Kjeldahl method and for total carbohydrates solved in 4.6 N

perchloric acid and estimated by Somogy's method.

Results and Discussion

Since shortday treatment given to IR-8 to hasten its flowering caused some abnormal growth, sometimes discussion on IR-8 was omitted.

For the lst week after anthesis, 1000-kernel-weight of both varieties increased most rapidly at mean temperatures around 30°C, while progressively decreasing at

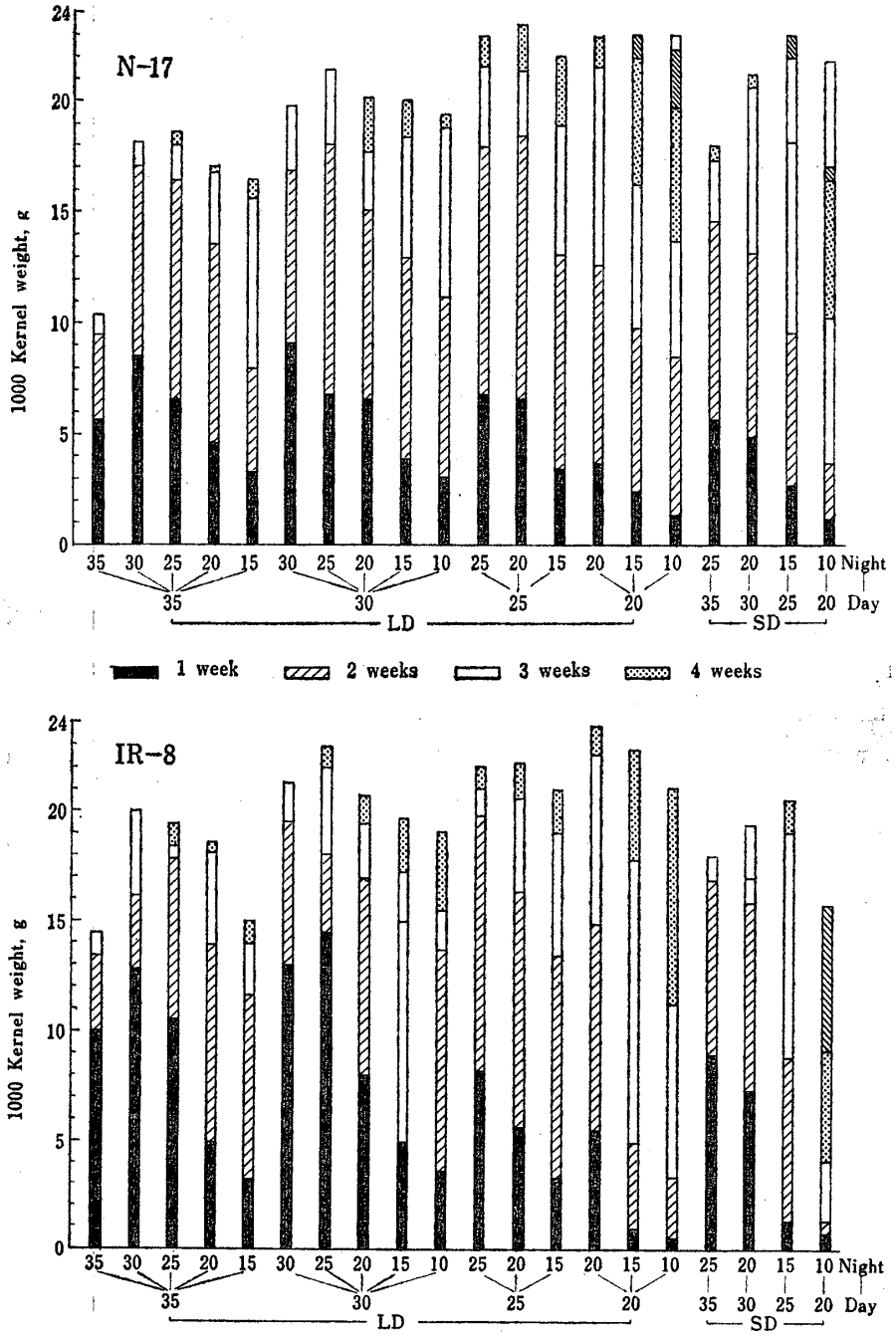

FIG. 1. 1000-kernel weight as determined by time (weeks after anthesis), day-night temperature and photoperiod

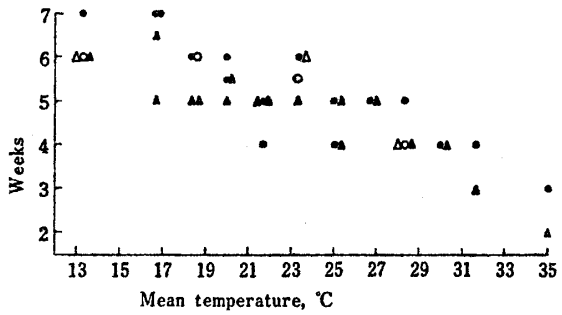

FIG 2. Maturation period (weeks) from anthesis to disappearance of green color of the hulls as affected by mean daily temperaures ● (LD), ○ (SD)-Norin-No. 17, ▲ (LD), △ (SD)-IR-8

lower temperatures. Higher temperatures than this, 35–35 and 35–30°C, also decreased the weight. For the 2nd week, however, the optimum mean temperature for increase of kernel weight became lower to 23–25°C. In general, it progressively decreased as the maturation proceeded (FIG. 1).

At higher temperatures maturation was hastened but ceased earlier resulting in lighter kernels, while at lower temperatures it was prolonged until the kernels were well-filled. At 35–30°C, for instance, maturation ended 2 to 3 weeks after anthesis, while at 20–10°C it took 6 to 7 weeks (FIG. 2). Taking no account of time, the optimum mean temperature for ripening may be as low as 20°C or a little lower for both varieties. These results substantially coincided with the earlier works (1–6).

Contrasting with Norin-17, IR-8 was less depressed in kernel-weight under higher mean temperatures, while under lower temperatures or extreme low night temperatures it was depressed more (FIG. 2). In both varieties the long-day condition was more favorable for ripening than the short-day condition (FIG. 1). There was a tendency for IR-8 to mature a little earlier than Norin-17 (FIG. 2).

The trend in 1000-kernel-weight had a close connection with the yellowing rate of the glumes (FIG. 3). Yellowing was most rapid at 30–30°C, followed by 35–30°C, and was delayed as the mean temperature or night-temperature lowered. At 35–35°C, the yellowing rate was farily slow especially in Norin-17. Like kernel-weight, the yellowing rate progressively increased as the ripening proceeded. At low temperatures such as 25–15, 20–15 and 20–10°C, the yellowing did not finish even at 6 weeks after anthesis. Rapid yellowing of IR-8 at 25–15°C seemed to be due to an abnormal senescence of the plant probably caused by an unknown disease. Short-day delayed yellowing more than long-day.

The lower leaves may die as the ripening proceeds partly ascribed to translocation of its material especially of nitrogen to panicle and partly because of the direct effect of the temperature. Fig. 4 shows the trend of green leaf number during ripening. In general, the leaves died earlier as the ripening rate increased, and at 30 and 25 day-temperatures they died earlier than those at 35 or 20°C where

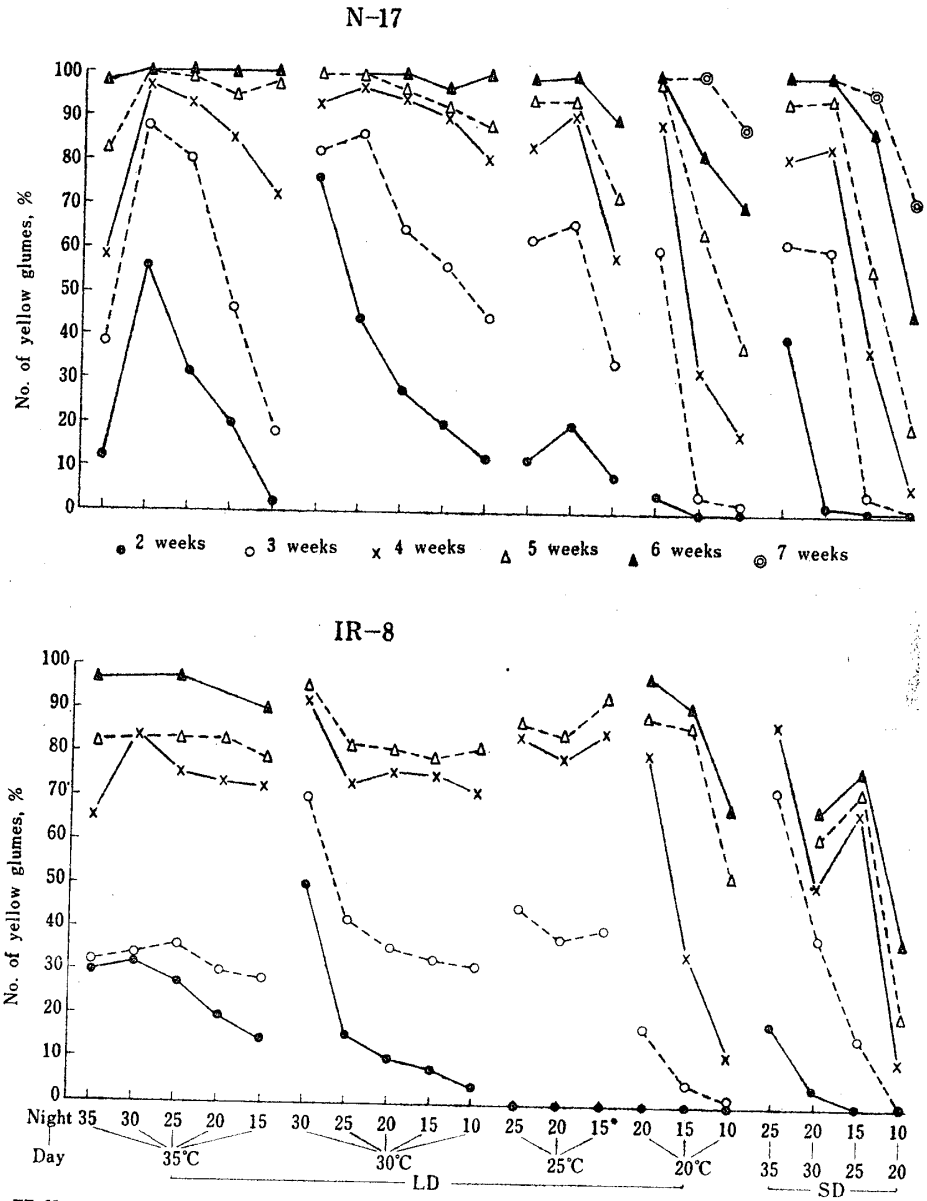

FIG 3. Yellowing rate of glumes as determined by time (weeks after anthesis), day-night temperature and photoperiod * abnormal senescence caused by disease

ripening was delayed for a longer period. At 35–35°C, new green tillers emerged from higher nodes (Pl. 1) during maturation, indicating an accumulation of some nutrients in the straw (8) as a result of an early termination of ripening. Even at 35°C day-temperature, leaves died more rapidly when night temperature dropped accompanied with a promotion of ripening. On the contrary, at 20°C day-temperature, the slower senescence of leaves coincided well with the slower but smooth ripening processes.

The fact that the senescence of Norin-17 leaves was slower at both 35–30 and 20–10°C in contrast to that of IR-8, may represent a varietal difference in resistance to extreme temperatures. Especially the early death of leaves of both varieties at

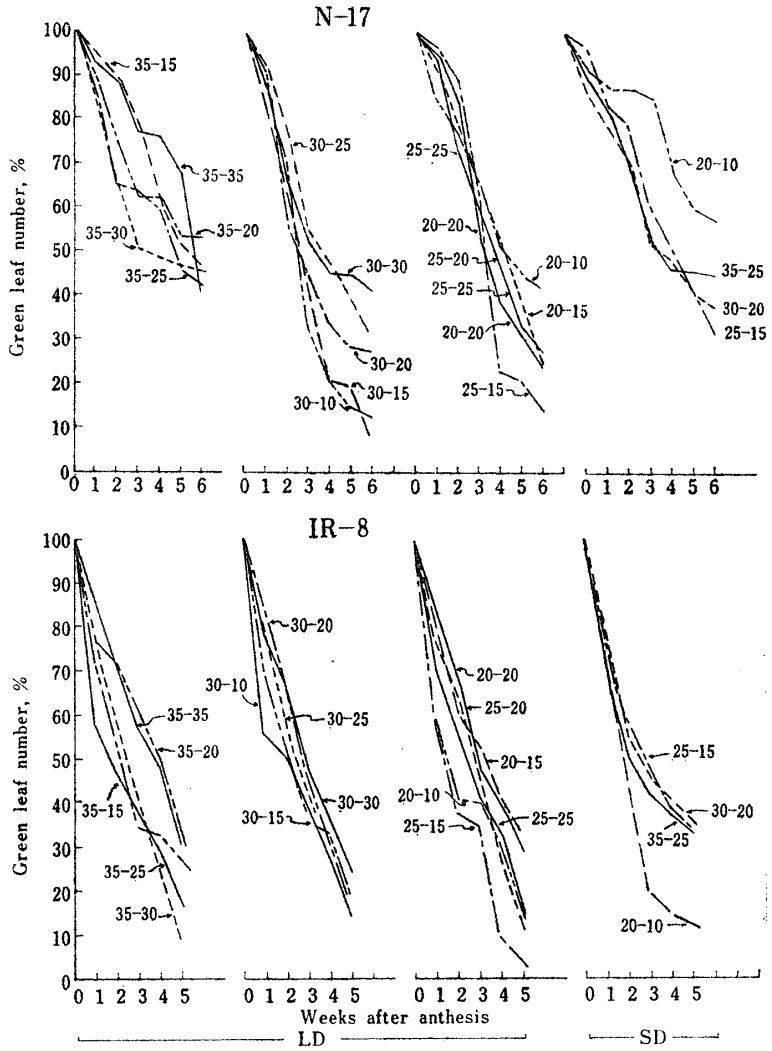

FIG. 4. Trend of green leaf number (% of that at anthesis) as influenced by day-night temperature and photoperiod

25–15°C may be attributed to some physiological abnormality the cause of which was not identified.

The 1000-kernel-weight and fruiting percentage at each maturity date of each plot are shown in Table 1. The plots with high 1000-kernel-weight and high fruiting percentage were 20–20, 20–15, 20–10 and 25–20°C in Norin-17, 20–20, 20–15 and 25–20°C in IR-8, respectively. It may be suggested from the results that the optimal mean temperature for ripening may be rather low, 13 to 20 and 17 to 22°C in Norin-17 and IR-8, respectively, although it took a longer time for maturation. The 1000-kernel-weight became successively smaller as the temperature raised above these optimums.

In this experiment the degree of fruiting was expressed by the product of the 1000-kernel-weight and the fruiting percentage, being tentatively named "ripening index". FIG. 5 shows these indices influenced by temperature and day-length,

TABLE 1. *The Effects of Photoperiod, Temperature and its Range on the Kernel Weight and Fruiting Percentage (F.P) at Each Maturity Date*

Variety		Norin-17					IR-8				
P.P	Day-Night °C	1000 kernel weight,g U*	M*	B*	Mean	F. P Mean	1000 kernel weight,g U*	M*	B*	Mean	F. P Mean
LD	35-35	13.0	10.7	6.5	10.4	92.2	14.7	11.0	6.9	10.5	89.6
	-30	17.3	16.4	15.7	16.5	97.3	20.1	15.0	10.4	14.9	93.0
	-25	17.5	16.9	14.9	16.5	95.0	19.5	18.5	11.9	16.8	72.0
	-20	16.9	14.6	12.0	14.6	97.5	17.8	14.8	13.0	15.2	84.6
	-15	15.9	15.3	15.6	15.6	97.5	14.9	13.9	10.0	13.3	78.2
	30-30	18.7	18.9	16.5	18.2	95.9	19.8	19.1	20.5	19.7	91.1
	-25	20.5	20.5	21.4	20.8	97.2	19.9	19.6	18.3	19.4	71.3
	-20	18.4	17.6	15.4	17.3	95.1	21.2	17.4	15.0	17.6	89.6
	-15	19.5	18.6	8.6	15.0	96.1	18.8	15.6	10.0	14.9	94.3
	-10	19.3	17.9	14.8	17.4	95.6	19.0	17.7	13.3	16.6	92.6
	25-25	21.3	21.3	20.2	21.0	97.8	21.1	20.2	15.5	19.1	96.5
	-20	21.8	21.6	21.1	21.6	98.0	22.0	22.3	20.6	21.7	92.2
	-15**	20.5	19.7	17.6	19.4**	92.9	20.9	18.9	12.8	17.7**	92.2
	20-20	22.3	22.6	21.4	22.2	99.0	23.5	24.8	23.9	24.2	96.0
	-15	22.7	22.5	20.3	21.9	96.6	23.9	24.3	24.3	24.2	96.0
	-10	23.2	22.5	17.7	21.5	97.1	22.9	22.1	19.2	21.3	87.6
SD	35-25	17.2	16.0	15.1	16.2	96.9	18.6	14.4	9.2	14.0	89.6
	30-20	20.1	19.8	21.1	20.2	97.8	17.6	14.7	12.2	14.7	92.8
	25-15	21.2	21.5	19.8	20.9	98.6	19.3	21.0	19.2	20.0	86.8
	20-10	20.9	21.3	20.7	21.0	96.8	17.1	12.9	5.7	12.0	87.6

Notes: P.P — Photoperiod U* — Upper part, M* — Middle part, B* — Basal part, of panicle ** Leaves died abnormally rapid, due to unknown disease damage

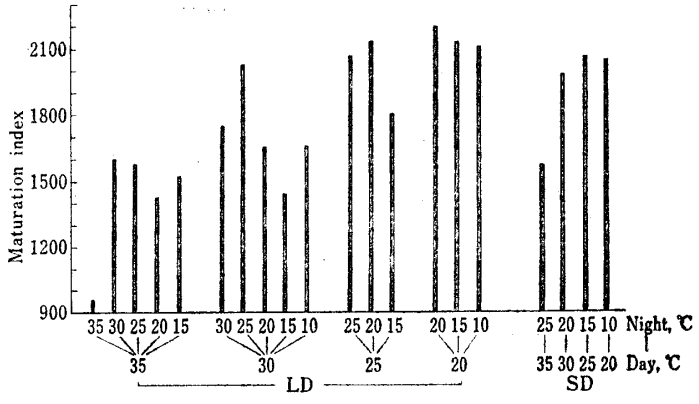

FIG. 5. Maturation index [1000-kernel weight (g) ×fruiting percentage (%)] as influenced by air temperature and photoperiod

illustrating the above conclusions more clearly.

At the same mean temperatures, the daily range of 5 to 10°C seems to be favorable for ripening. As shown in FIG. 6, the 1000-kernel-weight increased

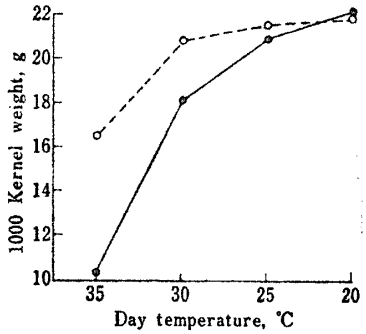

FIG. 6. Effects of temperature on the 1000-kernel-weight of Norin–17. Solid circle: night temperature is the same as day temperature. Empty circle: night temperature is 5° lower than the day temperature

as the mean daily temperature decreased. When the night-temperature was lowered 5°C than each day-temperature, the effect of dropping was more conspicuous at higher day-temperatures, being neglegible at lower day-temperatures.

In both varieties kernel weight at maturity decreased significantly at 35–35°C and showed much variability among kernels in a single panicle, being especially low at the lower part of it. Early flowering grains matured very early and the late flowering grains remained green even at harvest. In contrast, the kernels which

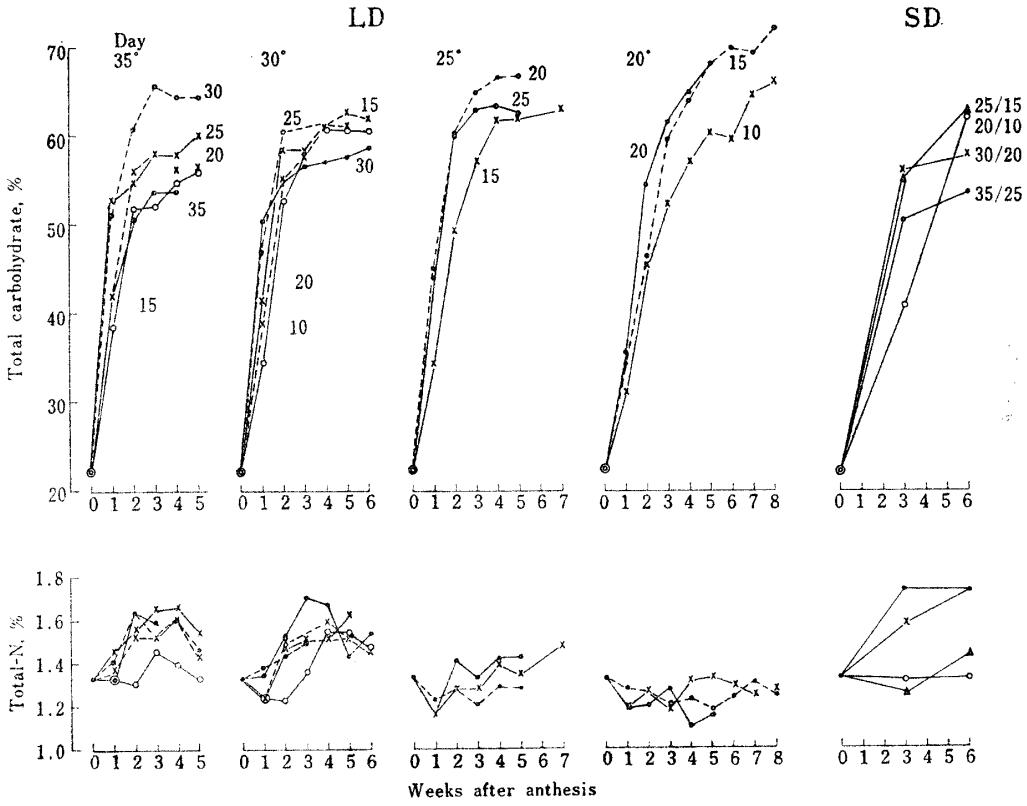

FIG. 7. Total carbohydrates and nitrogen accumulation in the panicle during ripening period as influenced by day-night temperatures and photoperiod (Norin–17)

matured at lower temperatures uniformly ripened with a high final 1000-kernel-weight, although it took much time until they turned yellow (Pl. 2).

As shown in FIG. 7, the carbohydrate concentration of the panicle increased parallel to the 1000-kernel-weight, being higher at lower day-temperatures with respective 5°C lower night-temperatures. Its accumulation decreased when both day- and night-temperatures were high, probably due greatly to the high consumption of carbohydrate by high respiration at night. The nitrogen concentration, on the contrary, became higher as day-temperature increased, except at 35 and 30°C with more than a 15°C daily range, where it became fairly low.

On the other hand, the nitrogen and carbohydrate concentrations in straw three or six after anthesis were lower at lower temperatures except 20–10°C, probably ascribable to the high translocation of these materials to panicle with a result of a higher "ripening index" (Table 2). The higher nitrogen and TAC contents at 20–10°C are closely connected with a slower rate of ripening and slower senescence of leaves (Fig. 3, 4).

The lower fruiting percentage, 1000-kernel-weight and their high variation in a single panicle at high temperatures may be partly induced by the lower amount of carbohydrate sent from the straw, caused by its much consumption by respiration, and thereby a greater competition for carbohydrate occurred among the

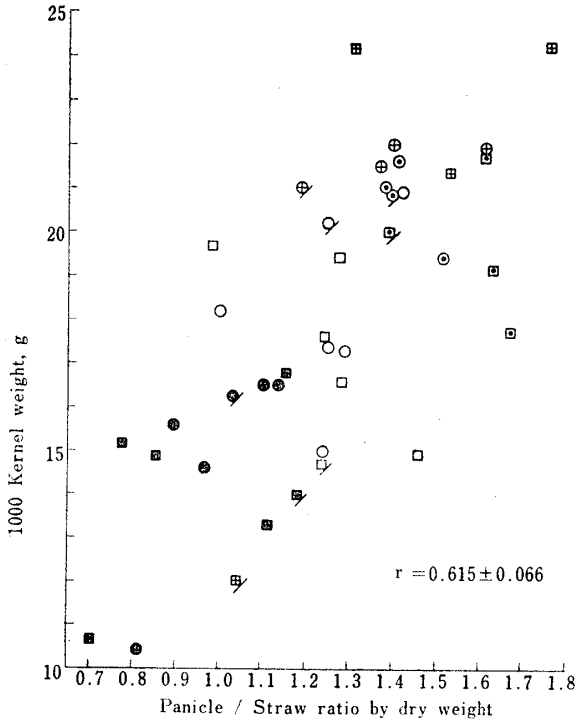

FIG. 8. Correlation between 1000-kernel weight and panicle/straw ratio by dry weight at maturity, each point representing one plot.

Daytemp.	35°	30°	25°	20°
Norin-17	●	○	⊙	⊕
IR-8	■	□	⊡	⊠

/ represents shortday plot.

TABLE 2. *Total Nitrogen and TAC (Total Sugar plus Crude Starch) Concentrations in the Straws at 3 and 6 Weeks after Anthesis as Influenced by Day-Night Temperatures under Longday Conditions (Norin-17)*

Day-Night °C	Total N, %		TAC, %	
	3 weeks	6 weeks	3 weeks	6 weeks
35-35*	1.02	0.67	5.09	5.81
-30	0.66	0.66	3.29	4.86
-25	0.53	0.69	3.27	4.33
-20	0.91	0.66	4.99	3.88
-15	0.99	0.64	4.99	6.00
30-30	0.83	0.60	2.28	3.54
-25	0.80	0.59	3.10	3.13
-20	0.74	0.59	2.36	3.02
-15	0.61	0.47	2.69	2.44
-10	1.03	0.49	2.96	2.87
25-25	0.62	0.51	2.95	2.95
-20	0.68	0.56	3.20	2.88
-15	0.76	0.59	3.06	2.85
20-20	0.60	0.57	4.76	5.86
-15	0.88	0.55	5.65	3.63
-10	0.88	0.75	7.94	6.60

* Newly emerged tillers removed

grains. Under very high temperatures such as 35–35°C, however, there was poor fruiting accompanied with greener straw, a low ratio of panicle to straw and many new tiller emergence, explaining the greater accumulation of nitrogen and TAC in the straw.

There was a positive correlation between the 1000-kernel-weight and ratio of panicle to straw as shown in Fig. 8, suggesting that the decrease of kernel-weight was caused not only by deficiency of carbohydrate but also by some fault in transolcation of the materials from straw to panicle. Regarding the translocation fault in higher temperature, Nakayama reported an early disappearnce of TTC reaction at the base of the grain, lowering of enzyme activity of endosperm and accumulation of sterole-like substance in the pedicel (7). These facts may be related to early senescence and an early termination of assimilates flowing into the grains as suggested by Matsushima and Wada (3). However these have been no causal explanations on the interrelation between carbohydrate deficiency and senescence of grains for which further studies are under way.

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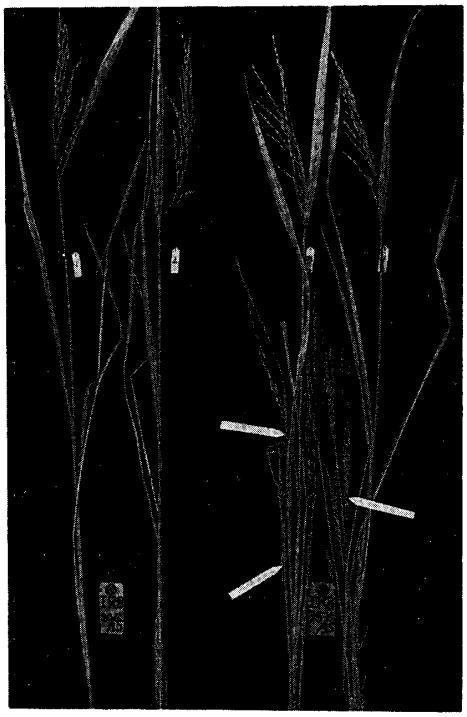
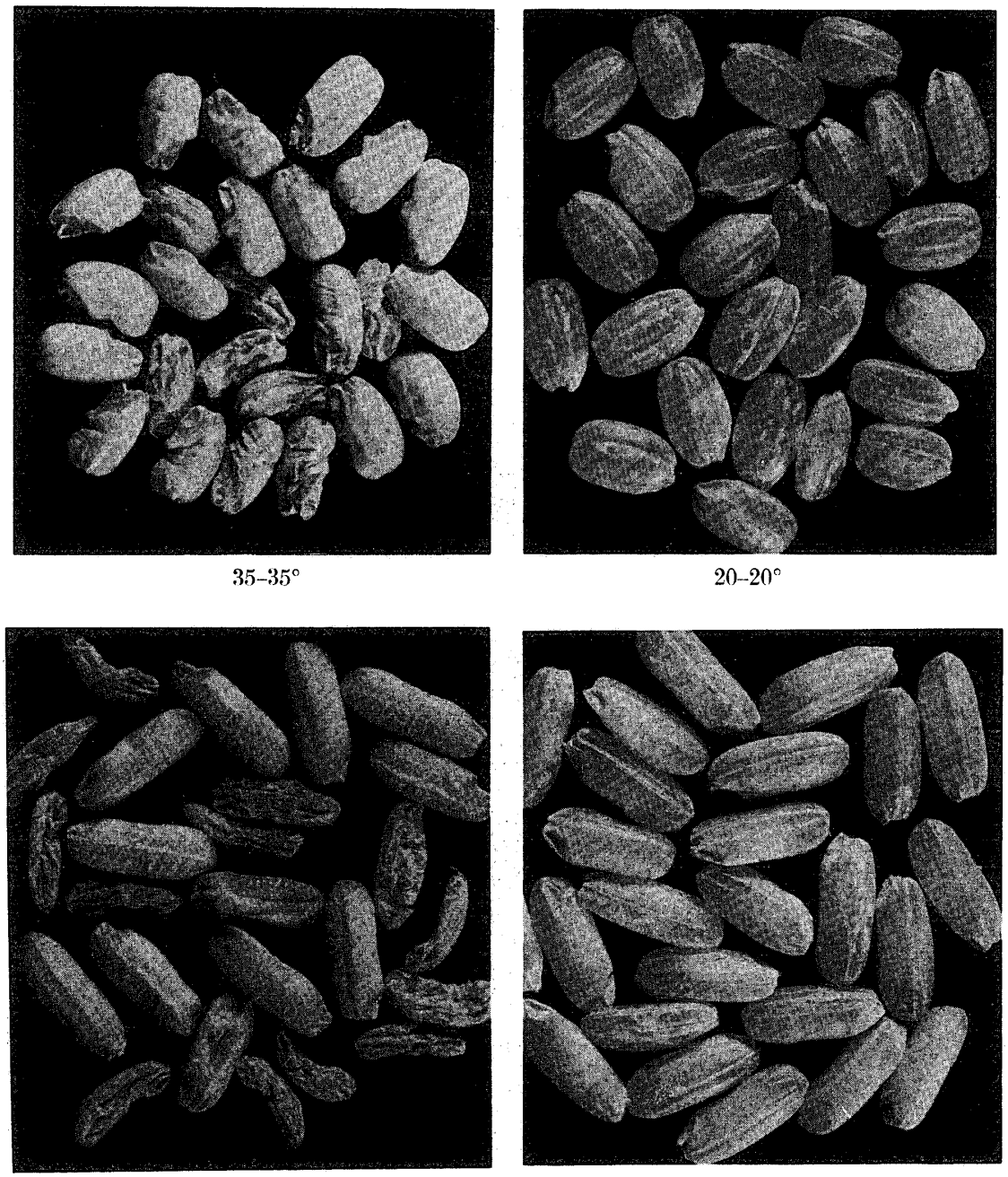


PLATE 1 New tiller emergence during ripening period at 35–35° (right) as contrasted with 20–15° where no tiller fromed (left) (IR–8) Arrows show new tillers

N-17



35-35° 20-20°

IR-8

PLATE 2 Examples of rice kernels ripened under different air-temperatures.